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ON THE CLASSIFICATION OF FROGS

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For nearly 30 years biologists rigorously adhered to Noble's (1931) classification of the frogs. Reig (1958) proposed subordinal categories, which only formalized the generally accepted "archaic" and "advanced" groups of families. Griffiths (1959a, 1959b) re-defined the types of pectoral girdles and made slight alterations in the standard classification. Griffiths' studies on the morphology of frogs culminated in a significant paper, "The phylogeny of the Salientia" (1963), in which major modifications in the classifications of frogs were proposed. Also in 1963, Hecht suggested changes in anuran classification on the basis of the phylogenetic importance of the larval types defined by Orton (1953), and Tihen (1965) summarized evolutionary trends in frogs. These papers, especially that by Griffiths (1963), seemed to provide the necessary catalyst for renewed interest in the evolutionary relationships of frogs.

The phylogenetic relationships at the familial level were re-evaluated by Inger (1967), Kluge and Farris (1969), and Lynch (1971). Salthe and Kaplan (1966) examined immunological evidence, and Morescalchi (1968, 1973) reviewed the karyological evidence. Diverse opinions on anuran phylogeny were presented at a symposium on the evolutionary biology of the anurans held at the University of Missouri at Kansas City in August, 1970; the results of the symposium have only recently been published (Vial, 1973). Among the collected papers in that volume, Estes and Reig (1973) surveyed the early fossil history of frogs, and Lynch (1973) proposed an evolutionary scheme for the transition from archaic to

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advanced frogs. Trueb (1973) synthesized the data on the evolution of skeletal features, and Starrett (1973) provided new interpretations of evolutionary patterns in tadpoles. Savage (1973) provided an exhaustive review of the geographic distribution of frogs and proposed a paleogeographic history in light of recent evidence on continental drift. Sokol (1975) presented detailed documentation of evolutionary trends in anuran larvae; his arguments demolished Starrett's (1973) scheme. Other evolutionary studies of various groups of frogs also have resulted in modifications of the taxonomy and phylogenetic placement of certain higher categories—Bufonidae (Trueb, 1971; McDiarmid, 1971; Blair, 1972), Leptodactylidae (Lynch, 1971), Dendrobatidae (Edwards, 1974; Silverstone, 1975), Rhacophoridae and Hyperoliidae (Liem, 1971), Hylidae (Duellman, 1970; Tyler, 1971), and Microhylidae (Zweifel, 1972).

As a consequence of these evolutionary studies, there is an array of changes in classification that are confusing to many systematists and incomprehensible to most non-systematists. Furthermore, four papers resulting from the symposium held in 1970 contain different classifications. Of these, Lynch (1973) has the most conservative classification; his studies were based primarily on adult morphology, but he discussed suprafamilial groups as "archaic," "transitional," and "advanced." Estes and Reig (1973) mostly relied on the conventional classification in their discussion of the fossil history of frogs. Starrett (1973) followed Hecht's (1963) suggested phylogenetic scheme and recognized four suborders based on Orton's (1953) larval morphology; Starrett's subordinal classification subsequently was nullified by Sokol (1975). In an attempt to reconstruct the evolutionary history of frogs on drifting continents with changing environments, Savage (1973) recognized 45 familial groups (families and subfamilies) within Starrett's subordinal arrangement. Thus, in one volume readers are faced with diverse phylogenetic schemes and resulting classifications. Are we to believe that tadpoles and frogs evolved independently? Or, should the evolution of a group be interpreted from morphology or geography? These questions are basic to the construction of a meaningful classification of the frogs.

The purpose of this paper is to provide a classification that is reasonably compatible with the evolutionary morphology of adults and larvae, and consistent with the continental configurations throughout the history of frogs. The basis for the classification essentially is a synthesis and re-evaluation of data in the literature plus some new data of my own. Hopefully this classification will provide some stability for reference by non-systematists and a basis for future modification by systematists.

CLASSIFICATION OF THE SALIENTIA

In the following classification I have used the subclass Lissamphibia. The higher classification of the Amphibia, especially as it relates to the origin of frogs, has been debated since Watson (1940). The paleontological evidence for the occurrence of a "proto-lissamphibian" stock in the Permian is now widely accepted (Carroll, 1964; DeMar, 1968; Bolt, 1969; Eaton, 1973). Estes and Reig (1973) discussed the early evolution of frogs with special reference to *Triadobatrachus* and the possibility of protolissamphibian evolution from within the dissorophid lissamphibians. A variety of evidence supports the common origin of the three Recent groups of amphibians (frogs, salamanders, and caecilians) from a lissamphibian ancestor (Eaton, 1959; Parsons and Williams, 1963; Szarski, 1962). However, Jarvik (1968) and Schmalhausen (1958) adhered to the older convention of diphyletic origin of the modern groups, and Wake (1970) and Wake and Lawson (1973) suggested a polyphyletic origin of the modern groups, based on the presumed evolution of the vertebrae.

I have not included subfamilies in the classification; their exclusion does not signify that I do not concede the subdivision of many families, especially Leptodactylidae and Microhylidae, into well-defined subfamilies. Instead this reflects inadequate knowledge of intrafamilial relationships in some large families, such as the Hylidae and Ranidae. Authorities for each taxonomic name have been designated as noted in Article 36 of the International Code of Zoological Nomenclature (1961). I have followed Fawcett

TABLE 1.—SHARED CHARACTER STATES OF 24 CHARACTERS IN THE SUPERFAMILIES OF FROGS. NUMBERS IN BOLDFACE ARE NUMBER OF CHARACTER STATES CONSTANT WITHIN THE SUPERFAMILY. NUMBERS TO THE LEFT OF THE BOLDFACE NUMBERS ARE THE MAXIMUM NUMBER OF STATES SHARED BETWEEN SUPERFAMILIES. NUMBERS TO THE RIGHT OF THE BOLDFACE NUMBERS ARE THE NUMBERS OF CHARACTER STATES CONSTANT WITHIN TWO SUPERFAMILIES.

	Discoglossoidea	Pipoidea	Pelobatoidea	Bufonoidea	Microhyloidea	Ranoidea
Discoglossoidea	21	9	14	6	9	10
Pipoidea	17	18	9	2	10	5
Pelobatoidea	19	18	20	9	10	12
Bufonoidea	15	15	21	15	14	12
Microhyloidea	11	14	14	19	24	14
Ranoidea	16	15	19	22	19	19

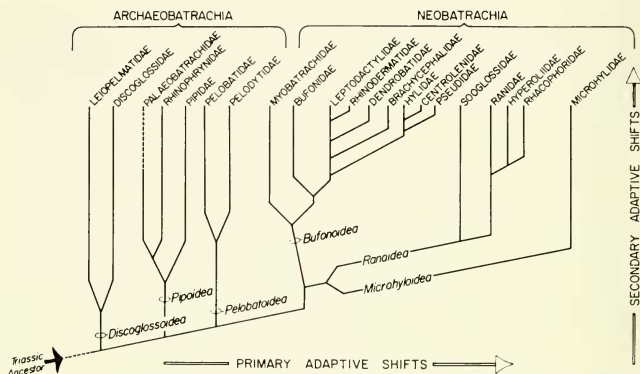


FIG. 1.—Phylogenetic arrangement of the Anura. Adaptive shifts are used in the sense of Trueb (1973).

and Smith (1971) in using Leioleptmatidae instead of Ascaphidae. Following the outline of the classification, each superfamily and family and suprafamilial category within the Anura is defined briefly, and the geographical distribution is given. In a final section various problematical taxa are discussed.

In constructing the classification I have attempted to group familial assemblages into suprafamilial categories on the criterion that families in one superfamily share more characters than does any of those families in another superfamily (Table 1). The average numbers of shared and constant character states within archaeobatrachian superfamilies are 18.0 and 10.8, respectively. Within neobatrachian superfamilies the numbers are 20.0 and 13.3, and between the Archaeobatrachia and Neobatrachia, 15.0 and 8.0. Simpson (1961:9) stated: "Zoological classification is the ordering of animals into groups (or sets) on the basis of their relationships, that is, of associations by contiguity, similarity, or both." The classification of frogs presented here reflects my concept of their phylogenetic relationships depicted in figure 1.

Class AMPHIBIA Linnaeus, 1758

Subclass LISSAMPHIBIA Haeckel, 1866

Superorder SALIENTIA Laurenti, 1768

Order †PROANURA Romer, 1945

Family †TRIADOBATRACHIDAE Kuhn, 1962

Order ANURA Giebel, 1847

Suborder ARCHAEOBATRACHIA Reig, 1958

- Superfamily DISCOGLOSSOIDEA Günther, 1858
 - Family LEOPELMATIDAE Mivart, 1869
 - Family DISCOGLOSSIDAE Günther, 1858
- Superfamily PIPOIDEA Bonapart, 1831
 - Family †PALEOBATRACHIDAE Cope, 1865
 - Family PIPIDAE Bonapart, 1831
 - Family RHINOPHYRIDAE Günther, 1858
- Superfamily PELOBATOIDEA Stannius, 1856
 - Family PELOBATIDAE Stannius, 1856
 - Family PELODYTIDAE Cope, 1866
- Suborder NEOBATRACHIA Reig, 1958
 - Superfamily BUFONOIDEA Gmelin, 1815
 - Family MYOBATRACHIDAE Schlegel, 1850
 - Family LEPTODACTYLIDAE Berg, 1838
 - Family BUFONIDAE Gmelin, 1815
 - Family BRACHYCEPHALIDAE Günther, 1858
 - Family RHINODERMATIDAE Günther, 1858
 - Family DENDROBATIDAE Cope, 1865
 - Family PSEUDIDAE Fitzinger, 1843
 - Family HYLIDAE Hallowell, 1857
 - Family CENTROLINIDAE Taylor, 1951
 - Superfamily MICROHYLOIDEA Parker, 1934
 - Family MICROHYLIDAE Parker, 1934
 - Superfamily RANOIDEA Linnaeus, 1758
 - Family SOOGLOSSIDAE Griffiths, 1963
 - Family RANIDAE Linnaeus, 1758
 - Family HYPEROLIIDAE Laurent, 1951
 - Family RHACOPHORIDAE Parker, 1934

ARCHAEOBATRACHIA

Vertebrae amphicoelous, opisthocoelous, or procoelous with labile intervertebral discs; ribs present or absent; pectoral girdle arciferous; scapula overlain by clavicle or not; *m. sartorius* not discrete from *m. semitendinosus*; amplexus inguinal.

DISCOGLOSSOIDEA

Presacral vertebrae 8 or 9, amphicoelous or opisthocoelous; sacral diapophyses moderately to broadly dilated; ribs present; scapula overlain or not by clavicle; tarsalia 3; tendon of *m. semitendinosus* inserting ventral to *m. gracilis*; pupil vertical or triangular; tadpoles having denticles and beaks, single median spiracle, no barbels.

Leiopelematidae.—Presacral vertebrae 9 (rarely 8), amphicoelous; *m. caudaliopuboischiotibialis* present; pupil vertical. Western North America and New Zealand.

Discoglossidae.—Presacral vertebrae 8 (rarely 9), opisthocoelous; *m. caudaliopuboischiotibialis* absent; pupil triangular (vertical in *Alytes*). Eurasia, North Africa, Philippines.

PIPOIDEA

Presacral vertebrae usually 8 (rarely 7), normally opisthocoelous (except *Palaeobatrachidae*); sacral diapophyses moderately to broadly dilated; free ribs present or absent in adults; pectoral girdle secondarily firmisternal in *Pipa*; scapula overlain by clavicle; tarsalia 2 or 3; tendon of *m. semitendinosus* penetrating *m. gracilis*; pupil vertical or round; tadpoles having paired spiracles and barbels, and no denticles or beaks.

†**Palaeobatrachidae.**—Presacral vertebrae 7 or 8, procoelous; first and second vertebrae fused; presacral vertebrae 7 and 8 or 7-9 fused; ribs free; parahyoid ossified; tarsalia 3; maxilla dentate; tongue?; pupil?; Jurassic-Pliocene, Europe.

Pipidae.—Presacral vertebrae 8, opisthocoelous; ribs free in subadults, ankylosed to transverse processes in adults (free in fossil genera); parahyoid ossified; tarsalia 2; maxilla edentate (edentate in some *Pipa*); tongue absent; pupil round. Africa, South America.

Rhinophrynidae.—Presacral vertebrae 8, opisthocoelous; ribs absent; parahyoid ossified; tarsalia 3; maxilla dentate; tongue present, free anteriorly; pupil vertical. Middle America.

PELOBATOIDEA

Presacral vertebrae 8 (rarely 9), procoelous with labile intervertebral cartilages in subadults and in some adult megophryine pelobatids; sacral diapophyses moderately to broadly dilated; ribs absent; scapula partially or not at all overlain by clavicle; maxilla dentate; tarsalia 2 or 3; tendon of *m. semitendinosus* inserting ventral to *m. gracilis*; pupil vertical; tadpoles having denticles and beaks, single sinistral spiracle, no barbels.

Pelobatidae.—Scapula not overlain by clavicle; tarsalia 2; astragalus and calcaneum separate. North America, Eurasia, Oriental region.

Pelodytidae.—Scapula partially overlain by clavicle; tarsalia 3; astragalus and calcaneum fused. Western Europe, Southwestern Asia.

NEOBATRACHIA

Vertebrae procoelous without labile intervertebral discs; ribs absent; pectoral girdle arciferous or firmisternal; scapula not overlain by clavicle; *m. sartorius* discrete from *m. semitendinosus*; amplexus inguinal or axillary.

BUFONOIDEA

Presacral vertebrae 8 (reduced to 7 in some); sacral diapophyses usually dilated; pectoral girdle usually arciferal (pseudofirmisternal) in rhinodermatids and some leptodactylids and bufonids, firmisternal in dendrobatids); tarsalia 2 or 3; tendon of *m. semitendinosus* usually inserting ventral to *m. gracilis* (penetrating *m. gracilis* in dendrobatids and some myobatrachids and leptodactylids, and dorsal to *m. gracilis* in some myobatrachids); pupil usually horizontal (vertical in some myobatrachids, leptodactylids, and hylids); amplexus axillary (inguinal in most myobatrachids and a few leptodactylids); tadpoles having denticles and beaks, single sinistral spiracle (except *Lepidobatrachus*, Leptodactylidae), no barbels.

Myobatrachidae.—Presacral vertebrae 8, first and second fused or not; maxilla normally dentate; phalangeal formula normal; small accessory head of *m. gluteus magnus* present. Australia and South Africa.

Leptodactylidae.—Presacral vertebrae 8, first and second maxilla normally dentate; phalangeal formula normal; accessory head of *m. gluteus magnus* present. South, Middle, and Southern North America, West Indies.

Bufonidae.—Presacral vertebrae 7 or 8, first and second fused or not, posterior vertebrae fused in some; maxilla edentate; phalangeal formula normal or reduced; accessory head of *m. gluteus magnus* present; Bidder's organ present. Cosmopolitan; not native to Australo-Papuan region.

Brachycephalidae.—Presacral vertebrae 7, first and second not fused; maxilla edentate; phalangeal formula reduced; accessory head of *m. gluteus magnus* present. Southeastern Brasil.

Rhinodermatidae.—Presacral vertebrae 8; first vertebra fused to second; pectoral girdle pseudofirmisternal; maxilla edentate; phalangeal formula normal. Southern South America.

Dendrobatidae.—Presacral vertebrae 8, first usually not fused to second; maxilla dentate or not; phalangeal formula normal; accessory tendon of *m. gluteus magnus* present. Tropical America.

Pseudidae.—Presacral vertebrae 8, first not fused to second; maxilla dentate; phalangeal formula increased by addition of ossified intercalary elements; accessory head of *m. gluteus magnus* present. South America.

Hylidae.—Presacral vertebrae 8, first not fused to second; pectoral girdle arciferal; maxilla dentate (except *Allophryne*); phalangeal formula increased by addition of intercalary cartilages; terminal phalanges claw-shaped (except *Allophryne*); astragalus and calcaneum not fused; accessory head of *m. gluteus magnus* absent. Cosmopolitan, except Ethiopian Region, Indian-Malayan Region, and East Indies.

Centrolenidae.—Presacral vertebrae 8, first not fused to second; maxilla dentate; phalangeal formula increased by addition of intercalary cartilages; terminal phalanges T-shaped; astragalus and calcaneum fused; accessory head of *m. gluteus magnus* absent. Tropical America.

MICROHYLOIDEA

Presacral vertebrae 8 (rarely 7) (eighth presacral vertebra procoelous or biconcave) sacral diapophyses broadly dilated; pectoral girdle firmisternal; tarsalia 2; tendon of *m. semitendinosus* dorsal to *m. gracilis*; pupil usually round; tadpoles having single, median spiracle, lacking denticles, beaks, and barbels.

Microhylidae.—Anterior pectoral girdle elements bony, cartilaginous, or absent; sacro-coccygeal articulation usually bicondylar; maxilla usually edentate; phalangeal formula normal (increased by addition of intercalary cartilages in phrynomerines). Ethiopian Africa, Madagascar, Oriental, Neotropical, Nearctic, and Australian regions.

RANOIDEA

Presacral vertebrae 8 (eighth presacral vertebra procoelus or biconcave); sacral diapophyses cylindrical (dilated in Sooglossidae); tarsalia 2 or 3; tendon of *m. semitendinosus* dorsal to *m. gracilis*; pupil horizontal (vertical in some hyperoliids); amplexus unknown in sooglossids; tadpoles having denticles and beaks, single sinistral spiracle, no barbels.

Sooglossidae.—Sacro-coccygeal articulation monocondylar; maxilla dentate; phalangeal formula normal; tarsalia 2. Seychelles Islands.

Ranidae.—Sacro-coccygeal articulation bicondylar; maxilla dentate or not; phalangeal formula normal; tarsalia 3. Cosmopolitan, except Southern South America and most of Australia.

Hyperoliidae.—Sacro-coccygeal articulation bicondylar; maxilla dentate; phalangeal formula increased by addition of intercalary cartilages; tarsalia 3. Africa, Madagascar, and Seychelles Islands (introduced).

Rhacophoridae.—Sacro-coccygeal articulation bicondylar; maxilla dentate; phalangeal formula increased by addition of intercalary cartilages; tarsalia 2. Africa, Madagascar, southeastern Asia.

SOME PROBLEMATICAL GROUPS

***Ascaplus-Leiopelma* Relationships.**—The North American *Ascapus* and the New Zealand *Leiopelma* have been placed in the same family by most students of anuran classification (Noble, 1931; Griffiths, 1963; Lynch, 1973). Savage (1973) in an unprecedented

move separated the two genera into different families; his motives were geographic, and he presented no new evidence to support his separation. Estes and Reig (1973) noted that the Jurassic ascaphids *Vieraella* and *Notobatrachus* from Argentina are intermediate between *Leiopelma* and *Ascaphus*, thereby further supporting the inclusion of the two Recent genera as relicts in the same family.

Ceratophryine Leptodactylids.—I have followed Lynch (1971) by including the genera *Ceratophrys*, *Lepidobatrachus*, and †*Wawelia* in the leptodactylid subfamily Ceratophryinae, rather than in a separate family, Ceratophryidae, as recognized by Cei (1965), Limeses (1964, 1965), Reig (1973), and Reig and Cei (1963). Among these authorities, Lynch is the only one who has compared the ceratophryine genera with all of the diverse genera of Leptodactylidae. On the bases of these comparisons, Lynch conservatively placed the ceratophryine genera in the Leptodactylidae, thereby suggesting that they are not so divergent from other leptodactylids as are other groups, such as bufonids.

Macrogenioglottus.—On the basis of Carvalho's (1946) description and evidence from other sources, Lynch (1971) placed *Macrogenioglottus alipioi* in *Odontophrynus*. Reig (1972) thoroughly reviewed *Macrogenioglottus* and concluded that it should be placed in a separate family, the *Macrogenioglottidae*, more closely related to the bufonids than to the leptodactylids. Obviously the status of this enigmatic genus is open to question.

Dendrobatidae.—Griffiths (1959b, 1963) considered the dendrobatids to be a Neotropical subfamily of ranids; this suggestion was based primarily on pectoral architecture and supposed "parallelisms" between dendrobatids and African petropedatine ranids. Lynch (1971) recognized the dendrobatids as a group derived from elosiine leptodactylids; his conclusions were based on the analysis of several suites of characters. Silverstone (1975) followed Lynch; it now is apparent that their conclusions are more tenable morphologically and zoogeographically than are Griffiths'.

Rheobatrachus.—Liem (1973) named the monotypic Australian frog *Rheobatrachus silus* and noted that it differed in many characters from other myobatrachids. Corben, Ingram, and Tyler (1974) reported that *Rheobatrachus* has a unique method of parental care; the embryos and tadpoles develop in the stomach, and the juveniles are propulsively ejected from the mouth. The presence of a combination of primitive morphological character states, which do not allow ready placement of the frog in either currently recognized myobatrachid subfamily in the Australo-Papuan region, nor the presence of a unique mode of life history (of which there is great diversity amongst bufonoids) does not preclude the inclusion of *Rheobatrachus* in the Myobatrachidae.

Geobatrachus.—The small fossorial frog, *Geobatrachus walkeri* Ruthven was originally placed in the Dendrobatidae, but Noble

(1931) and Griffiths (1959b) considered the species to be a leptodactylid. Lynch (1971) provided some evidence that *Geobatrachus* was not a leptodactylid and suggested that it might be a microhylid.

Specimens of *Geobatrachus* were collected in the Sierra Nevada de Santa Marta, Colombia, in June 1974. This fresh material provided the basis for the following observations: Presacral vertebrae 8, non-imbricate, bearing long transverse processes of equal length; sacral diapophyses flattened, not expanded; sacro-coccygeal articulation bicondylar; maxilla dentate; pectoral girdle firmisternal with clavicle and coracoid fused into bony plate; pre- and postzonal elements cartilaginous; cleithrum ossified and suprascapula cartilaginous; astragalus and calcaneum fused; tarsalia 2; phalangeal formula normal with T-shaped terminal phalanges; *m. sartorius* discrete from *m. semitendinosus*; tendon of *m. semitendinosus* inserting dorsal to *m. gracilis*; adult females having few, large, unpigmented eggs.

The combination of fused astragalus and calcaneum, T-shaped terminal phalanges, and firmisternal pectoral girdle is unique among anurans. The nature of the pectoral girdle is most like the condition seen in dendrobatids and is considerably different from that in *Rhinoderma* or in microhylids [relationships suggested respectively by Griffiths (1959b) and Lynch (1971)]. Pending the results of current studies on this frog by Charles F. Walker, I prefer not to make any familial assignment at this time.

Cochran and Goin (1970) described a tadpole from the Sierra Santa Marta that they tentatively assigned to *Geobatrachus walkeri*. Their description and illustration are almost certainly those of a *Centrolenella*, adults of which were unknown from the Santa Martas until 1974. The size and number of ovarian eggs in *Geobatrachus* suggests that the reproductive mode is one of terrestrial eggs undergoing direct development.

Allophryne.—Lynch and Freeman (1966) summarized the chaotic taxonomic history of this monotypic genus. The presence of an arciferal pectoral girdle and intercalary cartilages seems to ally this frog with either the Hylidae or Centrolenidae. But, it differs from hylids by having T-shaped terminal phalanges, from centrolenids by having the astragalus and calcaneum separate, and from both by having an edentate maxilla. Examination of recently acquired material confirms this suite of character states. The first observations on reproduction in *Allophryne ruthveni* were made by me in southeastern Venezuela in July 1974. Males were calling at night from vegetation over a temporary pond in rainforest. An amplexant pair deposited a clutch of approximately 300 small, pigmented eggs in water. Thus, the breeding behavior and reproductive mode are typically hylid, thereby lending support to Duellman's (1970) contention that *Allophryne* is a hylid; Savage (1973) recognized it as a separate monotypic family.

Australo-Papuan Hylids.—Tyler (1971) noted differences in the throat musculature in Australo-Papuan frogs formerly placed in *Hyla* and resurrected the generic name *Litoria* for these frogs. With the recognition of Australian "leptodactylids" as the Myobatrachidae, the monophyletic origin of the Hylidae is seriously questioned. Savage (1973) proposed that the Australo-Papuan genera be recognized as the family Pelodyadidae. This action emphasizes the need for further investigations on the hylids (*sensu lato*); until thorough comparative studies on hylid-leptodactylid, pelodyadid-myobatrachid, and pelodyadid-phyllomedusine relationships clarify the situation, the recognition of the Pelodyadidae offers little additional credibility to the classification of frogs.

Sooglossidae.—Griffiths (1959a) recognized *Nesomantis* and *Sooglossus* from the Seychelles Islands as a ranoid family Sooglossidae. Lynch (1973) considered the sooglossids as a transitional group. The characters of these frogs combine features usual to ranoids and bufonoids. The zoogeographic position of the sooglossids is closer to the ranoids, where I tentatively place them.

Microhylidae.—The structure of microhylid tadpoles has resulted in a controversy concerning the relationships of the family. Although Orton (1953) merely designated structural types of tadpoles, Hecht (1963) discussed taxonomic implications of larval types, and Starrett (1973) proposed subordinal names for the larval types. Savage's (1973) familial arrangement followed Starrett's subordinal classification. Lynch (1973), Trueb (1973), and Estes and Reig (1973) followed traditional classifications based primarily on characters of the adults. Starrett (1973) suggested that the larvae of microhylids have a suite of primitive characters; thus, the microhylids were recognized as a primitive suborder. However, Sokol (1975) demonstrated rather conclusively that the larvae are specialized derivatives of a more generalized type, such as present in the Bufonoidea and Ranoidea. Evidence from adult structure suggests that the microhylids are more closely related to ranoids than to other living frogs (Lynch, 1973, fig. 3-9). Recognizing these similarities, as well as the distinctive larvae, I have placed the microhylids in their own superfamily and suggest that they may be derived from an early stock that gave rise both to ranoids and microhylids.

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LITERATURE CITED

- BLAIR, W. F. (ed.). 1972. Evolution of the genus *Bufo*. Univ. Texas Press, Austin, viii + 459 pp.
- BOLT, J. R. 1969. Lissamphibian origins: possible Protolissamphibian from the Lower Permian of Oklahoma. *Science*, 166:888-891.
- CARROLL, R. L. 1964. Early evolution of dissorophid amphibians. *Bull. Mus. Comp. Zool., Harvard*, 131:163-250.
- CARVALHO, A. L. DE. 1946. Um novo genero de ceratophrydidea do sudeste bahiano. *Bol. Mus. Nac., N. S. Zool.*, 73:1-18.
- CEI, J. M. 1965. The relationships of some ceratophryid and leptodactylid genera as indicated by precipitin tests. *Herpetologica*, 20:217-224.
- COCHRAN, D. M., GOIN, C. J. 1970. Frogs of Colombia. *Bull. U.S. Natl. Mus.* 288:xii + 655.
- CORBEN, C. J., INGRAM, G. J., TYLER, M. J. 1974. Gastric brooding: unique form of parental care in an Australian frog. *Science*, 186:946-947.
- DEMAR, R. E. 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family *Dissorophidae*. *J. Paleo.*, 42:1210-1242.
- DUELLMAN, W. E. 1970. The hylid frogs of Middle America. *Monog. Mus. Nat. Hist. Univ. Kansas*, 1:1-753.
- EATON, T. H. JR. 1959. The ancestry of modern Amphibia: a review of the evidence. *Univ. Kansas Publ. Mus. Nat. Hist.*, 12:155-180.
- EATON, T. H. JR. 1973. A Pennsylvanian dissorophid amphibian from Kansas. *Occas. Papers Mus. Nat. Hist. Univ. Kansas*, 14:1-8.
- EDWARDS, S. R. 1974. A phenetic analysis of the genus *Colostethus* (Anura: Dendrobatidae). Unpub. Ph.D. Dissert. Univ. Kansas.
- ESTES, R., REIG, O. A. 1973. The early fossil records of frogs: a review of the evidence in Vial, J. L. (ed.). *Evolutionary biology of the anurans: contemporary research on major problems*. Univ. Missouri Press, Columbia: 11-63.
- FAWCETT, J. D., SMITH, H. M. 1971. Liopelmatina Mivart, 1869 (Amphibia, Salientia): Proposed emendation under the plenary powers to Leio- pelmatidae. *Bull. Zool. Nomencl.*, 28:50-52.
- GRIFFITHS, I. 1959a. The phylogenetic status of the sooglossinae. *Ann. Mag. Nat. Hist.*, (13)2:626-640.
- GRIFFITHS, I. 1959b. The phylogeny of *Sminthillus limbatus* and the status of the Brachycephalidae (Amphibia, Salientia). *Proc. Zool. Soc. London*, 132:457-487.
- GRIFFITHS, I. 1963. The phylogeny of the Salienta. *Biol. Rev.*, 38:241-292.
- HECHT, M. K. 1963. A reevaluation of the early history of the frogs. Part II *Syst. Zool.* 12:20-35.
- INGER, R. F. 1967. The development of a phylogeny of frogs. *Evolution*, 21: 369-384.
- JARVIK, E. 1968. Aspects of vertebrate phylogeny. in Ørving, T. (ed.). *Current problems of lower vertebrate phylogeny*. Almquist & Wiksell, Stockholm: 497-527.
- KLUGE, A. G., FARRIS, J. S. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.*, 18:1-32.

- LIEM, S. S. 1970. The morphology, systematics, and evolution of the Old World treefrogs (Rhacophoridae and Hyperoliidae). *Fieldiana, Zool.*, 57:vii + 145 pp.
- LIEM, S. S. 1973. A new genus of frog of the family Leptodactylidae from SE. Queensland, Australia. *Mem. Queensland Mus.*, 16:459-470.
- LIMESES, C. E. 1964. La musculatura del muslo en los ceratofrinidos y formas afines con un análisis crítico sobre la significación de los caracteres miológicos en la sistemática de los anuros superiores. *Cont. Cient. Ser. Zool. Univ. Buenos Aires*, 1:193-245.
- LIMESES, C. E. 1965. La musculatura mandibular en los ceratofrinidos y formas afines (Anura, Ceratophrynidae). *Physis*, 25:41-58.
- LYNCH, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas*, 53:1-238.
- LYNCH, J. D. 1973. The transition from archaic to advanced frogs. *in* Vial, J. L. (ed.). *Evolutionary biology of the anurans: contemporary research on major problems*. Univ. Missouri Press, Columbia: 133-182.
- LYNCH, J. D., FREEMAN, H. L. 1966. Systematic status of a South American frog, *Allophryne ruthveni* Gaige. *Univ. Kansas Publ. Mus. Nat. Hist.*, 17:493-502.
- MCDIARMID, R. W. 1971. Comparative morphology and evolution of frogs of the Neotropical genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*. *Sci. Bull. Nat. Hist. Mus. Los Angeles Co.*, 12:1-66.
- MORESCALCHI, A. 1968. Hypotheses on the phylogeny of the Salientia, based on karyological data. *Experimentia*, 24(9):964-966.
- MORESCALCHI, A. 1973. Amphibia. *in* Chiarelli, A. B. and E. Capanna (eds.). *Cytotaxonomy and vertebrate evolution*. Academic Press, London: 233-348.
- NOBLE, G. K. 1931. *The biology of the Amphibia*. McGraw-Hill Book Co. Inc., New York, 577 pp.
- ORTON, G. L. 1953. The systematics of vertebrate larvae. *Syst. Zool.* 2:63-75.
- PARKER, H. W. 1934. A monograph of the frogs of the family microhylidae. British Museum, London, viii + 208 pp.
- PARSONS, T. S., WILLIAMS, E. E. 1963. The relationships of the modern Amphibia: a re-examination. *Quart. Rev. Biol.*, 38:26-53.
- REIG, O. A. 1958. Propositiones para una nueva macrosistemática de los anuros. *Physis*, 21:109-118.
- REIG, O. A. 1972. *Macrogenioglottus* and the South American bufonoid toads. *in* Blair, W. F. (ed.). *Evolution in the genus Bufo*. Univ. Texas Press, Austin:14-36.
- REIG, O. A., CEI, J. M. 1963. Elucidación morfológico-estadística de las entidades del género *Lepidobatrachus* Budgett (Anura, Ceratophrynidae), con consideraciones sobre la extensión del Distrito Chaqueño del dominio zoogeográfico subtropical. *Physis*, 24:181-204.
- SALTHER, S. N., KAPLAN, N. O. 1966. Immunobiology and rates of enzyme evolution in the amphibia in relation to the origins of certain taxa. *Evolution*, 20:603-616.
- SAVAGE, J. M. 1973. The geographic distribution of frogs: patterns and predictions. *in* Vial, J. L. (ed.). *Evolutionary biology of the anurans: contemporary research on major problems*. Univ. Missouri Press, Columbia: 351-445.
- SCHMALHAUSEN, I. I. 1958 (1968). *The origin of terrestrial vertebrates*. Academic Press, New York, 314 pp.
- SILVERSTONE, P. A. 1975. A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. *Sci. Bull. Nat. Hist. Mus. Los Angeles Co.*, 21: 1-55.

- SIMPSON, G. G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York, xii + 247 pp.
- SOKOL, O. M. 1975. The phylogeny of anuran larvae: a new look. *Copeia*, 1975(1):1-24.
- STARRETT, P. H. 1973. Evolutionary patterns in larval morphology. *in* Vial, J. L. (ed.). Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia: 252-271.
- SZARSKI, H. 1962. The origin of Amphibia. *Quart. Rev. Biol.*, 37:189-241.
- THIEN, J. A. 1965. Evolutionary trends in frogs. *Amer. Zool.*, 5:309-318.
- TRUEB, L. 1971. Phylogenetic relationships of certain Neotropical toads with the description of a new genus (Anura: Bufonidae). *Contr. Sci. Nat. Hist. Mus. Los Angeles Co.*, 216:1-40.
- TRUEB, L. 1973. Bones, frogs, and evolution. *in* Vial, J. L. (ed.). Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia: 65-132.
- TYLER, M. J. 1971. The phylogenetic significance of vocal sac structure in hylid frogs. *Univ. Kansas Publ. Mus. Nat. Hist.*, 19:319-360.
- VIAL, J. L. (ed.). 1973. Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia, xii + 470 pp.
- WAKE, D. B. 1970. Aspects of vertebral evolution in the modern Amphibia. *Forma et Functio*, 3:33-60.
- WAKE, D. B., LAWSON, R. 1973. Developmental and adult morphology of the vertebral column in the plethodontid salamander *Eurycea bislineata*, with comments on vertebral evolution in the Amphibia. *Jour. Morph.*, 139:251-300.
- WATSON, D. M. S. 1940. The origin of frogs. *Trans. Roy. Soc. Edinburgh*, 60:195-213.
- ZWEIFEL, R. G. 1972. Results of the Archbold Expeditions. No. 97. A revision of the frogs of the subfamily Asterophryinae, family Microhylidae. *Bull. Amer. Mus. Nat. Hist.*, 148:411-546.